

Molecular mapping and characterization of traits controlling fiber quality in cotton

Russell J. Kohel, John Yu, Yong-Ha Park¹ & Gerard R. Lazo²

USDA-ARS, Crop Germplasm Research Unit, 2765 F&B Road, College Station, TX 77845, U.S.A.; ¹Permanent address: Korean Environmental Technology Research Institute, Kangnam-ku, Seoul 135-090, Korea; ²Permanent address: USDA-ARS, Western Regional Research Center, 800 Buchanan Street, Albany, CA 94710, U.S.A.

Received 20 January 2000; accepted 7 February 2001

Key words: cotton (*Gossypium hirsutum* L. and *G. barbadense* L.), fiber quality properties, quantitative trait loci (QTLs), random amplified polymorphic DNAs (RAPDs), restriction fragment length polymorphisms (RFLPs)

Summary

Cotton (*Gossypium* spp) is the world's leading natural fiber crop. Genetic manipulation continues to play a key role in the improvement of fiber quality properties. By use of DNA-based molecular markers and a polymorphic mapping population derived from an interspecific cross between TM-1 (*G. hirsutum*) and 3-79 (*G. barbadense*), thirteen quantitative trait loci (QTLs) controlling fiber quality properties were identified in 3-79, an extra long staple (ELS) cotton. Four QTLs influenced bundle fiber strength, three influenced fiber length, and six influenced fiber fineness. These QTLs were located on different chromosomes or linkage groups and collectively explained 30% to 60% of the total phenotypic variance for each fiber quality property in the F₂ population. The effects and modes of action for the individual QTLs were characterized with 3-79 alleles in TM-1 genetic background. The results indicated more recessive than dominant, with much less additive effect in the gene mode. Transgressive segregation was observed for fiber fineness that could be beneficial to improvement of this trait. Molecular markers linked to fiber quality QTLs would be most effective in marker-assisted selection (MAS) of these recessive alleles in cotton breeding programs.

Introduction

Cultivated cotton (*Gossypium* spp.) is the world's leading natural fiber crop and it is the cornerstone of textile industries worldwide. The cotton industry is confronted with problems in cost of production and requirements for high quality in the product. It is an industry in which cotton marketing is based on measurable quality factors and an industry in which technological changes are being implemented rapidly. All the changes in spinning technology have in common the requirement of greater fiber quality for their application to cotton (Deussen, 1992; Kohel, 1999ab). These factors require greater precision and speed to make genetic changes in cultivar development.

Fiber quality can be attributed by a set of the measurable properties that affect the spinning performance of the fiber. Among them, fiber strength, fiber length,

and fiber fineness are the primary quality properties that influence textile processing (Kohel, 1999b). However, their relative importance differs with various spinning technologies.

Highly productive Upland cottons (*G. hirsutum*) account for over 90% of lint production. The major disadvantage of Upland cottons has been the low fiber quality, compared to superior extra long staple (ELS) cottons (*G. barbadense*) (Kohel, 1999b; Benedict et al., 1999). The ELS cottons are prized for their superior quality fibers that allow processing into high-quality and high-valued yarns and fabrics. But the ELS cottons account for only a small fraction of the cotton production because of their low yield and limited adaptation to most cotton growing areas. For cotton growers to produce high-quality fiber required for increased textile automation, it is imperative to improve

the fiber quality while maintaining the fiber yield in the Upland cottons.

Genetic improvement continues to be key in meeting this agricultural challenge. Cotton fiber quality properties, as measured by fiber bundles, displays additive quantitative inheritance, which has facilitated a steady genetic advance in cotton improvement (Meredith, 1992; Kohel, 1999ab). However, identification of genetic factors responsible for such improvement has been difficult, limiting the efficiency of breeding efforts. Enhanced fiber quality properties may be due to either introgression of new genes or new combinations of existing genes (Kohel, 1999b). Genetic information and breeding methods available to cotton breeders have not allowed them to respond precisely to the needs of the textile industry for the desired combinations of fiber properties while maintaining high yield.

The emerging genomic technologies have revolutionized plant genetics and breeding (Tanksley et al., 1989; Phillips & Vasil, 1994). Plant genomic research has produced new molecular tools for agricultural scientists to improve breeding efficiency and accuracy. For example, the use of DNA markers for marker-facilitated selection brings extraordinary promise for streamlining many crop improvement efforts (Burr et al., 1983; Tanksley et al., 1988). DNA-based markers are phenotype-neutral, free of epistatic effects, and simply inherited Mendelian characters. DNA markers are particularly useful in introgression of valuable genes from exotic germplasm (Tanksley and McCouch, 1997) and breeding for traits affected by many quantitative trait loci (QTLs) (Edwards et al., 1987; Paterson et al., 1988).

DNA markers in cotton create unprecedented opportunities for improving this leading fiber crop. These molecular markers may be used to study genes controlling both simple and complex traits in cotton. With the construction of a molecular genetic map based on an interspecific cross between two improved cottons, *G. hirsutum* acc. TM-1 and *G. barbadense* acc. 3-79 (Yu et al., 1997), we have identified a number of DNA markers that are linked to fiber quality QTLs in ELS cotton 3-79. Relative gene effects of the identified QTLs for fiber strength, length, and fineness are also characterized herein.

Materials and methods

Mapping population

A segregating population consisted of 171 F₂ individuals from a cross between *G. hirsutum* acc. TM-1 and *G. barbadense* acc. 3-79, the genetic and cytogenetic standards for their respective species (Kohel, 1973). TM-1 is a long-term inbred (*S_n* generation, *n*>40) derived from the cultivar Deltapine 14 (Kohel et al., 1970). Modern Pima cottons are more productive, but their fiber quality does not exceed that of 3-79, a progenitor of the modern Pima germplasm. The unique high-quality fiber properties of the ELS cotton 3-79, and the high productivity and wide adaptability of Upland cotton TM-1, led to our choice of the mapping parents. These two day-neutral flowering cottons produced fertile F₁'s, and generated the polymorphic F₂ mapping population to identify quantitative trait loci for the fiber quality properties. The F₂ plants were maintained in the greenhouse as living specimens to produce seed, fiber, and leaf tissue for this mapping project.

Measurement of fiber quality properties

Individual cotton plants usually do not produce enough fiber for routine fiber measurements, especially for those of an interspecific hybrid population. To overcome the shortage of fiber, individual F₂ plants were grown as perennials in the greenhouse, and fiber samples large enough for analysis were obtained over multiple reproductive cycles. Fiber quality properties were considered to be free of significant genotype × year (*G* × *E*) interactions, and fiber measurements from both field and greenhouse were comparable (data not shown). Sampling of fibers over time from the greenhouse does not present a greater problem than any other form of replications in space. Bundle fiber quality properties for fiber strength, length, and fineness of the F₂ lint samples were determined by stelometer methodologies (StarLab, Knoxville, TN). The stelometer method of measurement was used over high volume instrumentation (HVI) methods to provide more precise measurements.

Assays of DNA markers

Cotton DNA was isolated from fresh young leaves. High levels of polyphenolics and other secondary compounds in cotton cells were removed with cetyltrimethyl-ammonium bromide (CTAB). Purified gen-

omic DNA was first evaluated for quality and quantity, and then used for analyses of two marker systems, restriction fragment length polymorphism (RFLP), and random amplified polymorphic DNA (RAPD). RFLP analysis followed standard liquid hybridization procedures (Yu et al., 1995; 1997). Hybridization probes included cotton genomic and cDNA clones obtained from Dr A.H. Paterson at Texas A&M University (Reinisch et al., 1994.) and Dr W.R. Meredith at USDA-ARS, Cotton Physiology and Genetics Research Unit (Shappley et al., 1996). Most of the cDNA clones used were developed by Biogenetic Service, Inc. in South Dakota. Four restriction enzymes *EcoRI*, *EcoRV*, *HindIII*, and *XbaI*, were used to digest the genomic DNA isolated from the mapping parents TM-1 and 3-79. Any one of the four enzymes detecting a polymorphism between TM-1 and 3-79 was used to digest the genomic DNA isolated from 171 F₂ progeny. A gel of 1.1% agarose in electrophoresis buffer (1 M Tris, 10 mM EDTA, 125 mM NaAc; pH 8.1) was used to separate DNA fragments. DNA transfer from the agarose gel to a blotting membrane was carried out overnight in alkaline transfer buffer (20 mM NaOH/0.6 M NaCl) after depurinating the gel in 0.25 M HCl for 10 minutes and then denaturing it in 0.4 N NaCl/1.5 N NaCl for 30 minutes. Prehybridization of UV cross-linked Southern blots were conducted at 65 °C in rotating glass bottles containing 5X SSPE, 5X Denhardt's, 1% SDS, and 100 ng/mL sheared salmon sperm DNA. A ³²P-labeled cotton probe was made according to random hexamer procedures (Feinberg and Vogelstein, 1984). After blots hybridized overnight with the ³²P-labeled probe, they were washed in steps of 2X SSPE/0.1% SDS, 1X SSPE/0.1% SDS, and 0.5X SSPE/0.1% SDS, respectively, before being exposed to X-OMAT films at -70 °C.

RAPD analysis followed traditional polymerase chain reaction (PCR) amplification procedures (Park and Kohel, 1993; Lazo et al., 1994). Random oligonucleotide primers (10-mer) were supplied by Operon Technologies (Alameda, California). Thermostable DNA polymerases were supplied by Perkin-Elmer Corp. (Norwalk, Connecticut) or Sigma (St. Louis, Missouri). PCR was conducted in 25 µl of a solution containing 2.5 µl of 10X PCR buffer (without MgCl₂), 0.2 mM each of dATP, dCTP, dGTP, dTTP nucleotides, 0.2 µM primer, 25 ng of cotton DNA. MgCl₂ concentration was adjusted to 1.5, 2.0, or 2.5 mM in the reaction mixture (Park and Kohel, 1993). *Taq* DNA polymerase was added at 0.5, 1.0 or 1.5 units in the

volume of 25 µl. Amplification was performed in a thermal cycler (GeneAmp PCR System 9600, Perkin-Elmer Corp.) programmed for 2 minutes at 95 °C and 45 cycles of 15 seconds at 94 °C, 30 seconds at 40 °C, 90 seconds at 72 °C, followed by 5 minutes at 72 °C. Amplified DNA fragments were resolved in 1.4% agarose gel using 1X TBE buffer. Any RAPD primers detecting a polymorphism between TM-1 and 3-79 were used to amplify the genomic DNA from 171 F₂ segregants.

Data analysis

Cotton DNA probes or random oligonucleotide primers were screened for their ability to detect a clear polymorphism between TM-1 and 3-79. Any probes or primers detecting a polymorphism were recorded and used to genotype 171 individual F₂ segregants derived from the TM-1 × 3-79 cross. Allotetraploid cotton usually had multiple DNA fragments hybridized with a single probe. A rule of 'double missing' was applied to identify dominant RFLP markers although most of them were codominant by nature. RAPD markers were dominant, and only unique DNA fragments were scored from the gel picture. Segregation data for both fiber quality parameters and polymorphic DNA markers were collected and stored in a programmable spreadsheet. DNA markers were placed on a linkage map by the program MapMaker/Exp ver. 3.0 (Lander et al., 1987; Lander & Bostein, 1989) running on a Sun SPARCstation 10 workstation. DNA markers or linkage groups were assigned to their respective cotton chromosomes using aneuploid cotton lines as described previously (Stelly, 1993; Yu et al., 1997).

The most widely applied QTL mapping method has been 'conventional' interval mapping (Lander and Botstein, 1989). QTLs for cotton fiber quality in the TM-1 × 3-79 population were identified using MapMaker/QTL version 1.1 (Lander et al., 1987). Regression analysis (SAS Institute, Cary, NC) was also used to identify DNA markers closest to the QTLs. This provided an additional check for QTLs in the marker intervals larger than 10 cM. Diagnostic DNA markers were identified for use in projects designed for marker-assisted selection (MAS) within the cotton breeding program. Both gene location and effect of the identified QTLs in 3-79 were analyzed in the genetic background of TM-1.

Nomenclature for the identified fiber quality QTLs was given tentatively (*t*) as fiber strength (*Sf*), fiber length (*Lf*), and fiber fineness (*Ff*). QTL

F ₂ distribution:				quartile	fraction within <i>n</i> deviations				
mean	sigma	skewness	kurtosis	ratio	1/4	1/2	1	2	3
22.75	2.67	0.11	0.06	1.08	0.24	0.37	0.64	0.95	0.99

17.41	*****
18.75	*****
20.08	*****
21.42	*****
22.75	*****
24.09	*****
25.42	*****
26.76	*****
28.09	*****
29.43	**

Figure 1. Fiber strength distribution among interspecific F₂ progeny, averaged over three reproductive cycles. Parental lines TM-1 and 3-79 had fiber strength measurements of 18.4 and 27.4 cN/tex, respectively.

mapping results were incorporated into workstation database management programs developed for the ongoing cotton genome project (<http://www.ars-genome.cornell.edu/>).

Results

Bundle fiber quality

Measurements of each quality property of fibers from both mapping parents and the F₂ progeny were averaged over three reproductive cycles at College Station, Texas. Upland cotton TM-1 had 18.4 cN/tex for fiber strength, 1.17 inch for fiber length, and 4.49 Micronaire units for fiber fineness. ELS cotton 3-79 had 27.4 cN/tex for fiber strength, 1.38 inch for fiber length, and 3.63 Micronaire units for fiber fineness. These represented almost 50% of improvement for fiber strength and about 20% for fiber length and fineness in ELS cotton 3-79 over TM-1. Fiber quality measurements of these parents from both field

and greenhouse were comparable, with slightly higher means and standard deviations in the field. The 171 F₂ progeny appeared to have a normal distribution of each of the three fiber quality properties (Figures 1, 2, and 3). The bundle fiber strength of the F₂ progeny ranged from 17.4 to 29.4 cN/tex, with a mean of 22.7 cN/tex. (Figure 1). The fiber length of the same F₂ progeny ranged from 1.06 to 1.41 inch, with a mean of 1.22 inch. (Figure 2). Fiber fineness ranged from 2.18 to 4.14 Micronaire units, with a mean of 3.05 Micronaire units where transgressive segregation was observed falling beyond ELS cotton 3-79 (Figure 3).

DNA marker analysis

The mapping parents, TM-1 and 3-79, were highly polymorphic at the DNA level. Approximately 75% of 300 cotton genomic and cDNA clones, probed on the parental survey blots, detected polymorphism with at least one of the four restriction enzymes: *EcoRI*, *EcoRV*, *HindIII*, and *XbaI*. Although some polymorphic DNA fragments comigrated and/or were

F ₂ distribution:				quartile		fraction within n deviations				
mean	sigma	skewness	kurtosis	ratio		1/4	1/2	1	2	3
1.22	0.08	-0.15	0.40	0.86		0.21	0.46	0.71	0.96	0.99

1.06 |****
 1.10 |*****
 1.14 |*****
 1.18 |*****
 1.22 |*****
 1.25 |*****
 1.29 |*****
 1.33 |*****
 1.37 |*****
 1.41 |*

Figure 2. Fiber length distribution among interspecific F₂ progeny, averaged over three reproductive cycles. Parental lines TM-1 and 3-79 had fiber length measurements of 1.17 and 1.38 inches, respectively.

nonallelic, most of RFLP markers were codominant and were used to genotype the F₂ segregants (Figure 4). Of 85 random primers that produced at least one polymorphic fragment, about 200 DNA fragments were generated to distinguish between TM-1 and 3-79. The size of these DNA fragments ranged from 250 to 3500 bp. RAPD markers were dominant and were used to genotype the F₂ segregants (Figure 5). A total of 355 DNA markers (216 RFLPs and 139 RAPDs) were assembled into 50 linkage groups, covering 4766 cm (Yu et al., 1998). Additional microsatellite (SSR) markers were also integrated to the map using the same F₂ progeny (Burr et al., unpubl.). The DNA markers and the linkage map were used to identify 13 quantitative trait loci (QTLs) that are responsible for fiber quality properties in ELS cotton 3-79.

QTLs for fiber strength

Tables 1a and 1b show 4 QTLs identified for bundle fiber strength (*Sf*). A suffix was added, '(t)', to sym-

bolize tentative assignments as *Sf-1(t)*, *Sf-2(t)*, *Sf-3(t)*, and *Sf-4(t)* on the basis of the ascending order of the cotton chromosomes (chr. 3b, chr. 14b, chr. 15a, and chr. 25b) where they were located. These QTLs collectively explained 35% of the phenotypic variance in the F₂ population (Tables 1a and 1b). One copy of *G. barbadense* 3-79 alleles of *Sf-1(t)* and *Sf-3(t)* in the *G. hirsutum* TM-1 genetic background increased fiber strength by 1.55 cN/tex, and 0.83 cN/tex, respectively. On the other hand, those of *Sf-2(t)* and *Sf-4(t)* decreased fiber strength by 0.27 cN/tex, and 1.75 cN/tex, respectively. *Sf-1(t)*, *Sf-2(t)*, and *Sf-3(t)* were recessive in their expression, while *Sf-4(t)* had additive to dominant effects (Table 1b). DNA markers closest to the QTLs were identified by regression analysis (Table 1a).

QTLs for fiber length

Tables 2a and 2b show 3 QTLs identified for bundle fiber length (*Lf*). These were also given tentative assignments with the '(t)' suffix added as *Lf-1(t)*, *Lf-2(t)*,

F ₂ distribution:				quartile		fraction within n deviations				
Mean	sigma	skewness	kurtosis	ratio		1/4	1/2	1	2	3
3.05	0.44	0.80	0.49	1.02		0.26	0.38	0.64	0.94	0.99

2.18 |*
2.40 |
2.61 |*****
2.83 |*****
3.05 |*****
3.27 |*****
3.49 |*****
3.71 |*****
3.92 |*****
4.14 |*****

Figure 3. Fiber fineness distribution among interspecific F₂ progeny, averaged over three reproductive cycles. Parental lines TM-1 and 3-79 had fiber fineness measurements of 4.49 and 3.63 Micronaire units, respectively.

Table 1a. Analysis of QTLs for fiber strength by ANOVA/GLM

Locus	DNA marker	Linkage group	R ²	P-value
<i>Sf-1(t)</i>	G3259	Chr. 3b	0.0999	0.0203
<i>Sf-2(t)</i>	AR038	Chr. 14b	0.0985	0.0128
<i>Sf-3(t)</i>	G2895	Chr. 15a	0.1006	0.0056
<i>Sf-4(t)</i>	C16A1b	Chr. 25b	0.1503	0.0011

Table 1b. Characterization of QTLs for fiber strength by MapMaker/QTL

Locus	Group	LOD	% Var.	a	d	d/a	Mode*
<i>Sf-1(t)</i>	Chr. 3b	2.20	15.4	1.547	-1.316	-0.851	RA
<i>Sf-2(t)</i>	Chr. 14b	2.08	10.4	-0.268	1.841	-6.869	RD
<i>Sf-3(t)</i>	Chr. 15a	2.69	14.9	0.834	-2.043	-2.450	RA
<i>Sf-4(t)</i>	Chr. 25b	2.68	23.1	-1.746	-0.791	0.453	AD

*A = Additive; D = Dominant; R = Recessive.

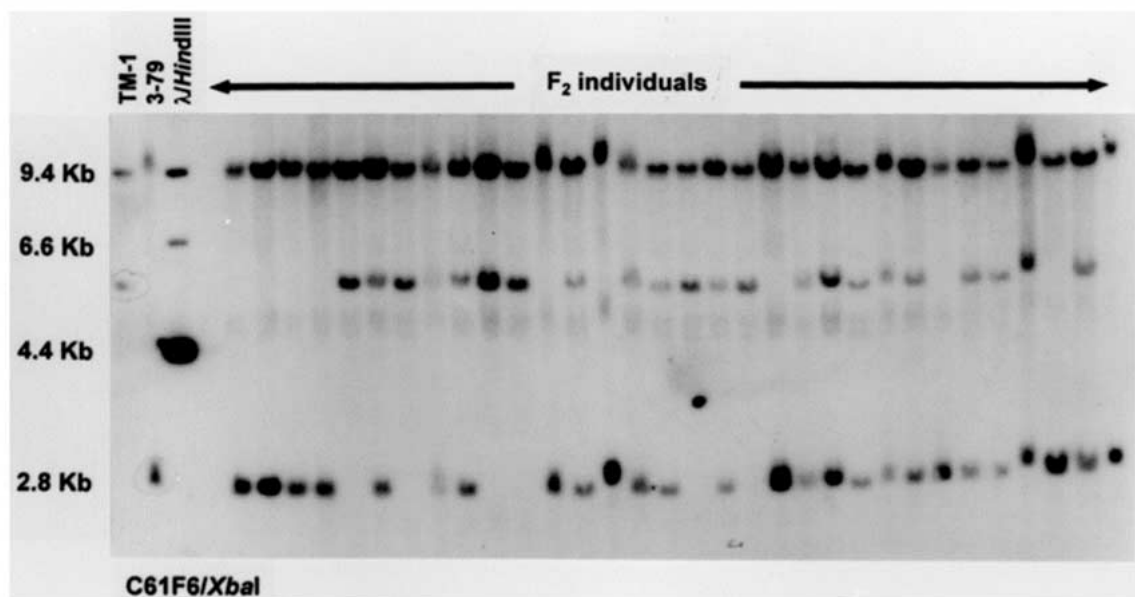


Figure 4. Segregation analysis of the F_2 progeny with C61F6, a cDNA clone. Total genomic DNA isolated from individual F_2 plants were digested with *Xba*I, a restriction enzyme detecting the polymorphism between TM-1 and 3-79, parents of the mapping progeny. In this case, C61F6 generated a codominant RFLP marker.

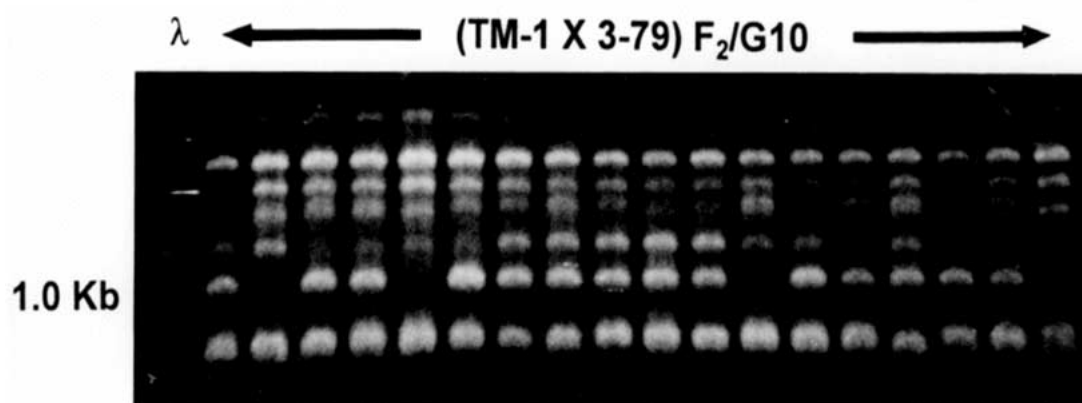


Figure 5. Segregation analysis of the F_2 progeny with G10, a 10-mer sequence synthesized from Operon Technologies, Inc. Total genomic DNA isolated from individual F_2 plants were amplified with the G10 primer. The amplified DNA fragments resolved in 1.4% agarose gel revealed 1.0-Kb dominant marker.

and *Lf-3(t)* on the basis of the ascending order of the cotton chromosomes (chr. 4a, chr. 18, and chr. 22) where they were located. These QTLs collectively explained about 30% of the phenotypic variance in the F_2 population (Tables 2a and 2b). One copy of *G. barbadense* 3-79 alleles of *Lf-1(t)* and *Lf-3(t)* in the *G. hirsutum* TM-1 genetic background increased fiber length by 0.007 inch and 0.019 inch, respectively. *Lf-2(t)* allele decreased fiber length by 0.006

inch in TM-1 background. *Lf-1(t)*, and *Lf-2(t)* were completely recessive while *Lf-3(t)* was recessive to additive in gene expression (Table 2b). DNA markers closest to the fiber length QTLs were identified in Table 2a.

QTLs for fiber fineness

Tables 3a and 3b show 6 QTLs for bundle fiber fineness (*Ff*). The '(t)' suffix was added to tentatively

Table 2a. Analysis of QTLs for fiber length by ANOVA/GLM

Locus	DNA marker	Linkage group	R ²	P-value
<i>Lf-1(t)</i>	G1010T	Chr. 4a	0.1020	0.0022
<i>Lf-2(t)</i>	G3029	Chr. 18	0.1467	0.0069
<i>Lf-3(t)</i>	C59E1	Chr. 22	0.0878	0.0175

Table 2b. Characterization of QTLs for fiber length by MapMaker/QTL

Locus	Group	LOD	% Var.	a	d	d/a	Mode*
<i>Lf-1(t)</i>	Chr. 4a	2.74	12.6	0.007	-0.052	-7.428	R
<i>Lf-2(t)</i>	Chr. 18	2.42	11.6	-0.006	0.052	-8.667	R
<i>Lf-3(t)</i>	Chr. 22	2.00	7.8	0.019	-0.033	-1.737	RA

*A = Additive; D = Dominant; R = Recessive.

assign identities as *Ff-1(t)*, *Ff-2(t)*, *Ff-3(t)*, *Ff-4(t)*, *Ff-5(t)*, and *Ff-6(t)* on the basis of the ascending order of the cotton chromosomes (chr. 1a, chr. 2a, chr. 3a, chr. 12b, chr. 16, and linkage group D1) where they were located. These QTLs collectively explained about 60% of the phenotypic variance in the F₂ population (Tables 3a and 3b). One copy of *G. barbadense* 3-79 alleles *Ff-3(t)*, *Ff-5(t)*, and *Ff-6(t)* in the *G. hirsutum* TM-1 genetic background reduced fiber Micronaire measurement by 0.36, 0.23, and 0.13 unit, respectively. Those of *Ff-1(t)*, *Ff-2(t)*, and *Ff-4(t)* increased fiber Micronaire measurement by 0.40, 0.27, and 0.16, respectively. *Ff-1(t)*, *Ff-2(t)*, and *Ff-4(t)* were recessive with minor additive effects for *Ff-4(t)* in their expression. In contrast, *Ff-3(t)*, *Ff-5(t)*, and *Ff-6(t)* behaved as dominants with *Ff-3(t)* exhibiting a minor additive effect (Table 3b). DNA markers closest to the fiber fineness QTLs are listed in Table 3a.

Discussion

Bundle fiber strength, length, and fineness are major fiber quality properties that are polygenic in inheritance (Kohel, 1999b; Yu et al., 1998). The measurement of fiber quality by bundle fibers provides the information for practical utilization and may be of use for future studies on cellulose biosynthesis in cotton fibers. A total of 13 QTLs identified in this study for bundle fiber strength (4), fiber length (3), and fiber fineness (6) on different chromosomes or linkage groups demonstrated polygenic inheritance of these properties. These QTLs collectively explained 30% to 60% of the total phenotypic variance for each

fiber trait in the F₂ population (Tables 1, 2, and 3). The effect and mode of action of the individual loci characterized in the genetic background of TM-1 indicated that most of the QTLs for fiber quality properties appeared to be recessive, making marker-assisted selection desirable and of great utility in fiber improvement. Three dominant loci (*Ff-3(t)*, *Ff-5(t)*, and *Ff-6(t)*) of ELS cotton 3-79 for fiber fineness may be transferred with greater ease into elite *G. hirsutum* cottons. The recessiveness of most *G. barbadense* 3-79 alleles responsible for bundle fiber strength, length, and fineness explains why introgression of fiber quality from *G. barbadense* into *G. hirsutum* in the past has been difficult (Kohel, 1999ab).

Attempts continue to be made to introgress some ELS genes into Upland cotton. DNA markers linked to fiber quality QTLs may facilitate marker-assisted selection in cotton breeding programs to engineer highly productive Upland cottons with superior quality of fiber strength, length, and fineness. DNA markers in Tables 1a, 2a, and 3a could serve as diagnostic tools for cotton breeders to follow fiber quality at seedling stages in early segregating generations. Even a 30% introgression of the ELS cotton (*G. barbadense*) genetic potential to Upland cottons (*G. hirsutum*) would be significant improvement in fiber quality. A few *G. barbadense* loci had a negative effect in *G. hirsutum*, which may be due to either different genetic backgrounds or interaction of genes between the two cotton species (Tables 1, 2, and 3). Results from characterizing QTLs of fiber quality properties should allow plant geneticists to investigate the origin of fiber qual-

Table 3a. Analysis of QTLs for fiber fineness by ANOVA/GLM

Locus	DNA marker	Linkage group	R ²	P-value
<i>Ff-1(t)</i>	C57A5	Chr. 1a	0.0859	0.0097
<i>Ff-2(t)</i>	C68C4	Chr. 2a	0.1178	0.0091
<i>Ff-3(t)</i>	P0953a	Chr. 3a	0.1206	0.0081
<i>Ff-4(t)</i>	F0911	Chr. 12b	0.1722	0.0027
<i>Ff-5(t)</i>	G3436	Chr. 16	0.1746	0.0026
<i>Ff-6(t)</i>	C38C1b	L.G. D1	0.1562	0.0016

Table 3b. Characterization of QTLs for fiber fineness by MapMaker/QTL

Locus	Group	LOD	% Var.	a	d	d/a	Mode*
<i>Ff-1(t)</i>	Chr. 1a	4.04	43.9	0.396	-0.328	-0.828	R
<i>Ff-2(t)</i>	Chr. 2a	3.79	31.8	0.274	-0.395	-1.442	R
<i>Ff-3(t)</i>	Chr. 3a	3.48	40.7	-0.357	-0.277	0.776	DA
<i>Ff-4(t)</i>	Chr. 12b	2.16	16.7	0.162	-0.218	-1.348	RA
<i>Ff-5(t)</i>	Chr. 16	3.03	17.4	-0.234	-0.301	1.286	D
<i>Ff-6(t)</i>	L.G. D1	3.19	21.3	-0.134	-0.401	2.993	D

*A = Additive; D = Dominant; R = Recessive.

ity genes, and the level of their expression in Upland cotton backgrounds.

Transgressive segregation is often observed in populations derived from interspecific crosses (deVicente & Tanksley, 1993). The occurrence of interspecific transgression may be due to induced mutation, gene complementation, and/or unlocking of the recessive genes (Rick & Smith, 1963). In this study, fiber fineness showed strong transgression in the progeny derived from the interspecific cross (TM-1 × 3-79). More than half of the F₂ individuals produced fibers that were finer than that of their ELS cotton parent 3-79 (Figure 3). The number of QTLs identified as contributing to fineness was larger than that of fiber strength and fiber length. QTLs with gene effects opposite to that predicted by the parental genotype could be, at least in part, associated with transgressive segregants (deVicente & Tanksley, 1993). For many important traits and characters in cotton such as fiber fineness, two distinct (but crossable) cultivated species (*Gossypium hirsutum* and *G. barbadense*) offer unique opportunities for interspecific transgression and complementation. The use of molecular markers provides tools to monitor transgressive variation and to facilitate interspecific introgression.

As demonstrated from the QTLs with opposite effects in this study, Upland cottons with relatively low-quality fibers do not necessarily lack all genes

for high-quality fibers in ELS cottons. Information is needed to understand whether *G. hirsutum* lacks critical genes for fiber quality, or whether it is mainly a problem of the different genetic backgrounds, or of gene interactions in two different cotton species. The basic questions cotton breeders often ask are which ELS genes for fiber quality are missing in the Upland cottons, and whether the ELS genes have the same expression in Upland cottons once they are introgressed. Currently, DNA markers already linked to the high-quality fiber properties in ELS cotton 3-79, and many more DNA markers in other genomic regions are used to initiate molecular mapping of fiber quality properties in two Upland cottons known to possess high-quality fiber. PD6992 has 25.7 cN/tex for fiber strength, 1.16 inch for fiber length, and 3.91 Micronaire unit for fiber fineness. HS427-10 has 27.8 cN/tex for fiber strength, 1.18 inch for fiber length, and 4.29 Micronaire unit for fiber fineness. Comparisons of gene locations and effects are to be made between ELS cotton 3-79 and Upland cottons PD6992 and HS427-10. We need to understand what genetic context a particular fiber quality QTL would likely be in for its maximal expression from one genetic background to another. We also need to know whether different fiber quality QTLs can complement one another to increase quality or interact to reduce it. Information from detailed mapping efforts would help

shed light on these important quality properties of the cotton plant.

Acknowledgements

We thank D.M. Stelly for the aneuploid cottons, and A.H. Paterson and W.R. Meredith for the cotton probes.

References

- Agricultural Statistics Board 1999 'Annual Crop Summary.' NASS, USDA Benedict, C.R., R.J. Kohel & H.L. Lewis, 1999. Cotton fiber quality, In: C.W. Smith & J.T. Cothren (Eds.), Cotton, pp. 269–288. John Wiley & Sons, NY.
- Burr, B., S.V. Evola, F.A. Burr & J.S. Beckmann, 1983. The application of restriction fragment length polymorphism to plant breeding. In: J.K. Setlow & A. Hollaender (Eds.), Genetic Engineering, vol. 5, Plenum Press, NY.
- Deussen, H., 1992. Improved cotton fiber properties: The textile industry's key to success in global competition. Symposium: Cotton Fiber Cellulose: Structure, Function, and utilization, pp. 43–63. National Cotton Council America, Memphis, TN.
- deVicente, M.C. & S.D. Tanksley, 1993. QTL analysis of transgressive segregation in an interspecific tomato cross. *Genetics* 134: 585–596.
- Edwards, M.D., C.W. Stuber & J.F. Wendel, 1987. Molecular-marker-facilitated investigations of quantitative trait loci in maize. I. Numbers, genomic distribution, and types of gene action. *Genetics* 116: 113–125.
- Feinberg, A. & B. Vogelstein, 1984. *Anal Biochem* 137: 266–267.
- Kohel, R.J., 1973. Genetic nomenclature in cotton. *J Hered* 64: 291–195.
- Kohel, R.J., 1999a. Cotton Improvement: A Perspective. Cotton World 1: (in press).
- Kohel, R.J., 1999b. Cotton germplasm resources and the potential for improved fiber production and quality, In: A.S. Basra (Ed.), Cotton Fibers, pp. 167–182. The Haworth Press, Inc, NY.
- Kohel, R.J., T.R. Richmond & C.F. Lewis, 1970. Texas Marker-1. Description of a genetic standard for *Gossypium hirsutum* L. *Crop Sci* 10: 670–671.
- Lander, E.S. & D. Botstein, 1989. Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. *Genetics* 121: 185–199.
- Lander, E.S., P. Green, J. Abrahamson, A. Barlow, M.J. Daly, S.E. Lincoln & L. Newburg, 1987. MAPMAKER: An interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. *Genomics* 1: 174–181.
- Lazo, G.R., Y.H. Park & R.J. Kohel, 1994. Identification of RAPD markers linked to fiber strength in *Gossypium hirsutum* and *G. barbadense* interspecific crosses. *Proc Biochemistry of Cotton*. September 28–30, 1994. Galveston, Texas.
- Park, Y.H. & R.J. Kohel, 1994. Effect of concentration of MgCl₂ on random amplified DNA of cotton. *BioTechniques* 16: 652–656.
- Paterson, A.H., E.S. Lander, J.D. Hewitt, S. Peterson, S.E. Lincoln & S.D. Tanksley, 1988. Resolution of quantitative traits into Mendelian factors, using a complete linkage map of restriction fragment length polymorphisms. *Nature (London)* 335: 721–726.
- Reinisch, A.J., J. Dong, C.L. Brubaker, D.M. Stelly, J.F. Wendel & A.H. Paterson, 1994. A detailed RFLP map of cotton. *Gossypium hirsutum* × *G. barbadense*: Chromosome organization and evolution in a disomic polyploid genome. *Genetics* 138: 129–147.
- Rick, C.M. & P.G. Smith, 1953. Novel variation in tomato species hybrids. *Am Nat* 88: 359–373.
- Shappley, Z.W., J.N. Jenkins, C.E. Watson Jr, A.L. Kahler & W.R. Meredith Jr, 1996. Establishment of molecular markers and linkage groups in two F₂ populations of upland cotton. *Theor Appl Genet* 92: 915–919.
- Stelly, S.M., 1993. Interfacing cytogenetics with the cotton genome mapping effort. *Proc Beltwide Cotton Improv Conf*, pp. 1545–1550.
- Tanksley, S.D., J.C. Miller, A.H. Paterson & R. Bernatzky, 1988. Molecular mapping of plant chromosomes, In: J. Gustafson & R. Appels (Eds.), Chromosome Structure and Function, pp. 157–172. Plenum Press, NY.
- Tanksley, S.D., N.D. Young, A.H. Paterson & M.W. Bonierbale, 1989. RFLP mapping in plant breeding: new tool for an old science. *Biotechnology* 7: 257–264.
- Tanksley, S.D. & S.R. McCouch, 1997. Seed banks and molecular maps: unlocking genetic potential from the wild. *Science* 277: 1063–1066.
- Yu, Z.H., J.F. Wang, R.E. Stall & C.E. Vallejos, 1995. Genomic localization of tomato genes that control a hypersensitive reaction to *Xanthomonas campestris* pv. *vesicatoria* (Doidge) Dye. *Genetics* 141: 675–682.
- Yu, Z.H., Y.-H. Park, G.R. Lazo & R.J. Kohel, 1997. Molecular mapping of the cotton genome. *Proc of 5th International Congress of Plant Molecular Biology*. September 21–27, 1997. Singapore.
- Yu, Z.H., Y.H. Park, G.R. Lazo & R.J. Kohel, 1998. Molecular mapping of the cotton genome: QTL analysis of fiber quality characteristics. *Proc of Plant Animal Genome VI*, Jan 18–22, 1998. San Diego California.